Pergamon

PII: S0042-6989(97)00106-5

Vision Res., Vol. 37, No. 23, pp. 3417–3426, 1997

Printed in Great Britain
0042-6989/97 $17.00 + 0.00

A Glimpse into Crabworld

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Received 29 October 1996; in revised form 13 March 1997

Almost all known arthropod compound eyes exhibit regional variations of resolving power, absolute light, spectral and polarisation sensitivity which are likely to be matched to the probability of significant events and the availability of cues in the visual world. To understand the signal processing requirements that have led to the evolution of matched sensory and neural filters, we thus need a detailed description of the input signals to a visual system and of the tasks to be performed under natural operating conditions. We report here on the first steps we took in an attempt to reconstruct an animal's specific visual world with emphasis on the motion domain. Fiddler crabs (genus *Uca*) live in burrows on sand- and mudflats and are active during low tide. They carry their eyes on long, vertically oriented stalks and use vision to detect predators and conspecific signals generated by males waving one massively enlarged claw. The crabs sit on the ground plane of a flat world, where significant events are most likely to occur in a narrow band around the horizon. We recorded scenes in a crab colony with a video camera at crab eye height. The salience of relevant features in the spatial, spectral and polarisation domains was analysed in digitised video images and short sequences of film were processed by a two-dimensional network of motion detectors at various spatial scales. The output of the network provides us with histograms of the direction and strength of motion signals in various spatio-temporal frequency bands. We discuss our results in terms of detection problems, predictability of events, global vs local information content and higher level motion processing involved in intraspecific communication.

Fiddler crabs Visual ecology Matched filters Motion detection model Image statistics

INTRODUCTION: VISION IN A FLAT WORLD

The world does not look the same everywhere, and eyes do not sample the world in a uniform fashion like a camera. Distortions of the sampling array in biological systems are the rule rather than the exception, no matter what optics may be involved. Depending on environmental geometry, closely related animals may possess rather different retinae, suggesting that the sensory periphery is matched to the statistics of the animal's visual world. Tree kangaroos, for instance, have a concentric fovea, while plains kangaroos possess a visual streak (Hughes, 1975). The theme of matched retinal filters can be most convincingly developed by considering the visual systems of arthropods (e.g. Wehner, 1987; Land, 1989). There are two reasons for this: the first is a technical one, in that the regional variation of properties are comparatively easy to study in compound eyes and the second has to do with many arthropods showing very specific adaptations to the principal constraints for visual processing in specific environments. In practically every compound eye we find that the distribution of resolving power, of absolute, spectral and polarisation sensitivity is not uniform across the visual field.

Regional variations in the optical and receptive properties of eyes remind us that already at the front-end, visual systems can be special-purpose built. Adaptations are often related to specific tasks the animals have to perform, like chasing small objects (Land, 1989), navigating with the aid of a compass (Wehner, 1989), or locating water (Schwind, 1995). Amongst these specialisations, equatorial acute zones stand out, in that they are specifically related to the local topography of the environment the animals inhabit. They are found in intertidal crabs that live on sand- and mudflats (Horridge, 1978; Zeil *et al.*, 1986, 1989), in waterstriders that live and hunt on the water surface (Dahmen, 1991), but also in quite a large number of vertebrates (Hughes, 1977). A flat world has a distinct visual structure, the ground plane being imaged onto the part of the retina serving the ventral visual field, the horizon onto the eye equator and the sky onto the dorsal visual field. Apart from this highly predictable geometry there are clear constraints as to where in the visual field significant events are likely to happen. For a crab or any observer sitting on the ground plane, the world from a distance of five body heights to infinity is compressed into a 10 deg-wide horizontal slice of the visual field and it is more or less in this narrow sector that predators need to be distinguished from

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conspecifics, males from females and comparatively larger conspecifics from smaller ones. Except for predators approaching from above, all other events that are relevant to a flatworld crab or a plain-dwelling kangaroo are likely to happen within the equatorial region of visual space and, because of geometry, the cues by which it can make vital discriminations are even further constrained. For instance, a crab sees everything that is larger than itself above the line of horizon (Zeil *et al.*, 1986; Land & Layne, 1995; Layne *et al.*, 1997). In addition, the closer objects are on the ground plane, the lower they appear in the visual field. Interestingly, most conspecific signals in flatworld crabs, from the waving displays of male fiddlers to the sand pyramids of ghost crab males, all seem to be designed to penetrate the horizon line (Salmon & Hyatt, 1983), suggesting that they are mimetic signals, ironically tapping into the females' predator warning system (Christy, 1995; Land & Layne, 1995). The statistics of the scenes in which flatworld crabs operate are thus highly non-uniform on all levels of analysis: ambient light intensities and spectral composition differ between the ventral and dorsal visual field, as does the spatial frequency content and the distribution of polarised light. The probability of events relevant to a crab is also not the same throughout visual space. As argued above, the "biological information content" is much higher in the equatorial slice viewing the horizon than anywhere else. In addition, the predictability of events is different in horizontal and vertical directions, in that a crab cannot predict *where in azimuth* along the horizon relevant events are likely to happen, but if they occur, they will announce themselves within the equatorial visual field.

The specialisations of the visual system in flatworld crabs reflect this predictable structure of visual space: specifically, it is *vertical* resolving power which is increased in equatorial acute zones (Zeil *et al.*, 1986; Land & Layne, 1995) and the gradient of vertical resolution is flatter in the ventral compared with the dorsal visual field (Zeil & Al-Mutairi, 1996). The control systems stabilising the eyes are appropriately tuned to the situation in a flat world: the acute zone is aligned visually with the local horizon (Nalbach *et al.*, 1989; Zeil, 1990; Zeil & Al-Mutairi, 1996) and the optomotor sensitivity for horizontal motion shows a narrow maximum in the part of the visual field just above the eye equator, where contours are likely to be far away (Nalbach & Nalbach, 1987).

We are interested in quantifying the visual ecology of flatworld crabs with the broader aim of characterising the selective pressures that may have shaped their visual system. As an initial step we attempt to describe the visual environment of crabs by recording scenes in crabworld from the viewpoint of the animal and by subsequently analysing digitised video images in terms of the animal-relevant information they contain. With this approach we hope eventually to be able to characterise the detection and discrimination problems the animals face, and to identify both the cues crabs use, and the sensory and neural filters that allow them to extract vital information from visual input.

MATERIALS AND METHODS

Recording

Scenes were filmed in fiddler crab colonies of *Uca lactea annulipes* in Kuwait, and of *Uca vomeris* in Queensland, Australia. A Sony Video-8 Camcorder with a standard zoom lens that could be equipped with colour and polarising filters was placed at crab eye height, with the lens centre about 2.5 cm off the ground. For calibration of viewing angle a 10 cm high object was positioned at 57 cm distance. Video-8 films were copied onto VHS tapes and digitised with 8 bit resolution and 512×512 pixel image size for later analysis.

Motion analysis

For motion analysis, short sequences of video film covering a 42 deg × 30 deg field of view were digitised at lower resolution and stored as images of 256×256 pixel size. Pairs of successive video half-frames were averaged, leading to a temporal resolution of 25 frames per second. An episode of 1.4 sec (36 frames), showing a group of crabs moving on the ground, was analysed in detail by passing it through a two-dimensional network of motion detectors. The motion detector model which we used was developed for interpreting human motion perception and is referred to as 2DMD (Zanker, 1996).

The basic building blocks of the 2DMD model are elementary motion detectors (EMDs) of the correlation type (for review, see Reichardt, 1987; Borst & Egelhaaf, 1989). This model, used here only as representative of luminance-based motion detectors, has been widely applied in the context of insect vision and human perception, but could be replaced by other models without changing the major results (van Santen & Sperling, 1985; Adelson & Bergen, 1985). In a simple implementation (see inset in Fig. 2), each EMD receives input from two points of the spatially filtered stimulus patterns, which interact in a nonlinear way after some temporal filtering to provide a directionally selective signal. DOGs (Difference of gaussians) were used as bandpass filters in the input lines, with excitatory center and inhibitory surround balanced so as to exclude any DC components from the input (cf. Srinivasan & Dvorak, 1980). To prevent aliasing, the diameter of the receptive field (as measured between zero-crossings from excitatory to inhibitory regions) was set to about twice the sampling distance between the two inputs. This sampling distance was used as a fundamental *spatial* model parameter, and varied between 2 and 16 pixels. The signal from one input line was multiplied by the temporally filtered signal from the other line, and two antisymmetric units of this kind were subtracted from each other, with equal weights leading to a fully opponent EMD. This kind of detector is highly directionally selective. The time constant of the first-order lowpass filter was used as a fundamental *temporal* model

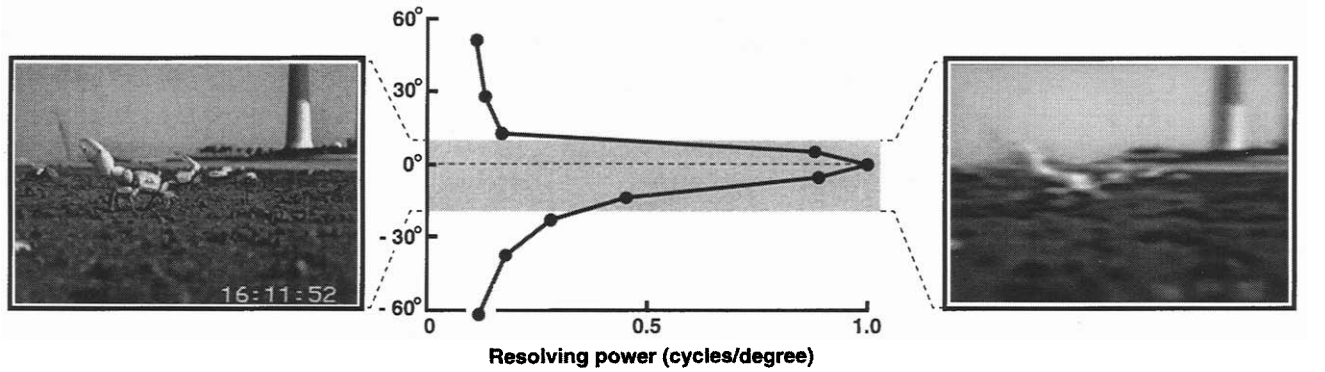

FIGURE 1. A video image from crab eye height is shown on the left. The diagram in the centre shows a sagittal profile of resolving power with elevation in degrees on the y-axis. The grey-shaded area marks the part of the profile covered by the scene and that was used to generate the filtered version on the right. The video image was filtered along horizontal rows with a gaussian of $\sigma = 0.665$ deg (half the horizontal interommatidial angle) and along columns using a gaussian with σ depending on elevation according to $\sigma = 0.0025\ (\alpha * n - \eta)^2 + 0.25$ (with $\alpha = 0.058$ deg, the vertical angular size of pixels; $n = 1,..., 511$, the pixel row number; $\eta = 12.1$ deg, the angular position of the horizon relative to the top edge of the image). The intensity value of each pixel in the filtered image was divided by the vertical resolution at that position before normalizing the whole image to maximum. In this crude way, the variation of lens diameters and absolute sensitivity which approximately follows the profile of resolution close to the eye equator is accounted for. The filter values and the equation to model the variation of vertical resolution are taken from Zeil & Al-Mutairi (1996).

parameter, and set to eight simulation steps, which corresponds to the duration of 1 frame. At a frame rate of 25 Hz this time constant corresponds to 40 msec, which would lead to a temporal frequency optimum of 4 Hz, which is well within the range of temporal frequency characteristics of a variety of motion-sensitive neurones in arthropods (O'Carroll *et al.*, 1996).

The sequences of stimulus frames were processed by two 2D-arrays of such correlators (two sets of 256×256 EMDs), which were either oriented along the horizontal or along the vertical axis of the computer images. This leads to a two-dimensional motion signal distribution, the 2DMD output, with pairs of horizontal and vertical components for each image point. In some cases this raw 2DMD output was subjected to local averaging (across an area of 4×4 sampling distances), or to temporal averaging (over 8 frames) before further analysis. The 2D-maps of motion responses were converted into two-dimensional histograms by digitising the local EMD responses at 8 bit resolution, and by counting the number of occurrences of a given pair of horizontal and vertical responses. The histograms are scaled relative to maximum signal strength so that the majority of response magnitudes are accommodated. The zero bin was excluded from analysis because it usually contains a huge number of counts from the static image regions.

RESULTS

Lowpass to crabworld and the "information content" of scenes

Fiddler crabs have panoramic vision with fairly constant resolution along the horizontal direction and an acute zone with increased vertical resolving power centred on the horizon. What does the world look like through such an "astigmatic" compound eye? In Fig. 1 we show a scene from crab eye height, and the same view filtered with crab eye resolution (see also von Uexküll & Brock, 1926; Land & Layne, 1995). The maximal resolving power of the fiddler crab eye is about 0.4 c/deg in the horizontal and 1–1.5 c/deg in the vertical direction (Land & Layne, 1995; Zeil & Al-Mutairi, 1996). Not surprisingly, the distribution of light intensities we see after such filtering is a lowpass filtered version of the original scene, which, however, still retains quite detailed information on the locations and relative sizes of the crabs on the substrate. The fact that the scene is viewed by an equatorial acute zone is not immediately obvious so that a detailed scene analysis will be required to detect its functional significance in terms of the image processing advantages it may convey. It needs to be stressed at this point that the filtered scene represents nothing more than what is left after the image has passed the optics of the compound eye. It is not what the crab "sees", but what the crab's brain has to work with in terms of spatial resolution. We are, in addition, only looking at an 8-bit greylevel representation of the distribution of ambient light so that the potentially relevant spectral and polarisation characteristics of the scene, which we will discuss later, are lost.

The image in Fig. 1, however, allows us to define what we mean by the "biological information content" of natural scenes. The visual system of fiddler crabs has a limited number of *detection* and *discrimination* tasks to perform. The list for low-level detection tasks would be (1) sky–substrate contrast; (2) object–sky contrast; (3) object–substrate contrast; and for the discrimination tasks, the list would run like this: (1) predator/conspecific; (2) nearby/far away; (3) larger/smaller conspecific; (4) male/female. To quantify the image processing requirements of these visual tasks, we ideally

need radiometrically calibrated images across the visible and ultraviolet spectrum, so that the available signals can be described in terms of differences in photon arrivals at the eyes of a crab. So far, calibrated images are beyond our reach, but what we can do at this rather qualitative stage is to measure the contrast of animal-relevant features in the scenes and to explore how crabs may use image motion cues for detection and discrimination purposes. For instance, the bodies of the three crabs closest to the camera in the centre of the image in Fig. 1 all appear as bright areas below the line of the horizon. Depending on their distance they lie at a different elevation in the visual field and differ in angular size. The question then becomes how reliably other crabs can be detected in the intensity distribution that is passed by a crab's compound eye and to what degree the differences in retinal elevation and angular size can be discriminated. Equally, since the camera was at crab eye height when the scene was recorded, the raised claws of the two closest crabs penetrate the horizon line. At least in the still greylevel image there is little intensity difference between the raised claws and the celestial background so that object–sky contrast becomes an issue, again requiring calibrated images to be tackled. The still image of Fig. 1 is deceptive, however, in that the crabs in the scene are in continuous motion, both moving about and signalling by waving their enlarged claw. In the next section we will analyse these motion signals and the motion patterns they generate in more detail.

Who moves where and how?

Notwithstanding their musical name, one important means of communication in fiddler crabs is visual motion signals. The enormously enlarged and often brightly coloured claw in males has probably evolved partly to boost visual signal strength. In the waving displays performed by males during territorial interactions and when attempting to attract a female, they rhythmically raise the claw high above the carapace. The displays differ amongst species in the path the claw takes, the speed and the rhythm of waves (Salmon & Hyatt, 1983). Motion signals in the context of communication thus require of the receiver quite complex mechanisms for the detection and discrimination of motion patterns. In a first attempt to describe the motion detection problems fiddler crabs have to cope with during communication, we analysed a video sequence containing such characteristic waving displays at various viewing distances. This procedure neglects any movements of the observer, i.e., it exclusively refers to the situation when a crab sits still and just watches the scene, and we are well aware that we are looking only at one isolated aspect of crab motion vision. To analyse how the retrievable motion signals reflect the choreography of the scene, we will present frequency histograms of the 2DMD output, as well as two-dimensional maps of motion signal distributions at various spatial scales.

We first address the mere occurrence of motion signals of various strength and direction at different spatial scales. Figure 2 shows two-dimensional histograms, in which the greylevel corresponds to the frequency of occurrence of a motion signal with a given direction and strength (see inset). The image in the top left corner of Fig. 2 shows one frame of the sequence in which the crab in the foreground starts lifting its left claw and lowers a leg on its right side, whereas another crab in the background moves its claw to the left (indicated by arrows). The four *columns* of histograms represent the distributions of motion signals at four different spatial scales, with EMD sampling distances ranging from 2 to 16 pixels (corresponding to 0.23–1.83 deg in vertical direction). The four *rows* of histograms refer to different treatments of the raw 2DMD output signals, as specified at the right-hand-side of each row. Many of the histogram entries scatter around the zero bin and have to be considered as motion noise from which the signal has to be separated. This motion noise is partially due to the imperfect stabilisation of the image, and partially due to the inherent properties of the EMD. The local EMD output (in space and time) does not faithfully represent the veridical motion, and only after some spatial or temporal averaging does a reliable motion signal emerge (cf. Egelhaaf *et al.*, 1989; Zanker, 1996).

As may be expected from the limitations at the elementary level of motion detection, the distribution of the raw motion signals, at each spatial scale, is rather broad (first row of Fig. 2). In fact, it is very difficult to discriminate the characteristic movement components—the lifting of the claws—from the overall noise in the scene, because there is only a mild shift of the centre of gravity of the distribution in the direction of the upper right corner. It is only at the two medium spatial scales that a tendency in favour of the top right quadrant becomes apparent in the 2D-histograms. The peak corresponds to the claw movement in the right upward direction. This property of the signal distribution emerges very clearly from the histogram when the 2DMD output signals are averaged locally (second row in Fig. 2)—a strategy which improves the performance in discrimination tasks considerably (Zanker, 1996). Again, the best representation of the claw movement appears at the two medium spatial scales. With a sampling base of 8 pixels, another prominent motion component becomes discernible, with symmetrical histogram components slightly tilted counterclockwise from the vertical orientation. The additional component, which is barely noticeable in the other histograms, corresponds to a tiny jitter in the whole image owing to imperfect frame grabbing. No attempt was made to compensate for frame jitter because it can be considered to mimic the consequences of the kind of small scanning movements that have been observed in crabs around the vertical eye axis (Sandeman, 1978). Temporal averaging over the eight frames of the sequence also helps to segregate the behaviourally relevant signal (third row of Fig. 2) and leads to prominent motion components in the upper right quadrant of the histogram. Interestingly, temporal averaging is not as efficient as local spatial averaging in this

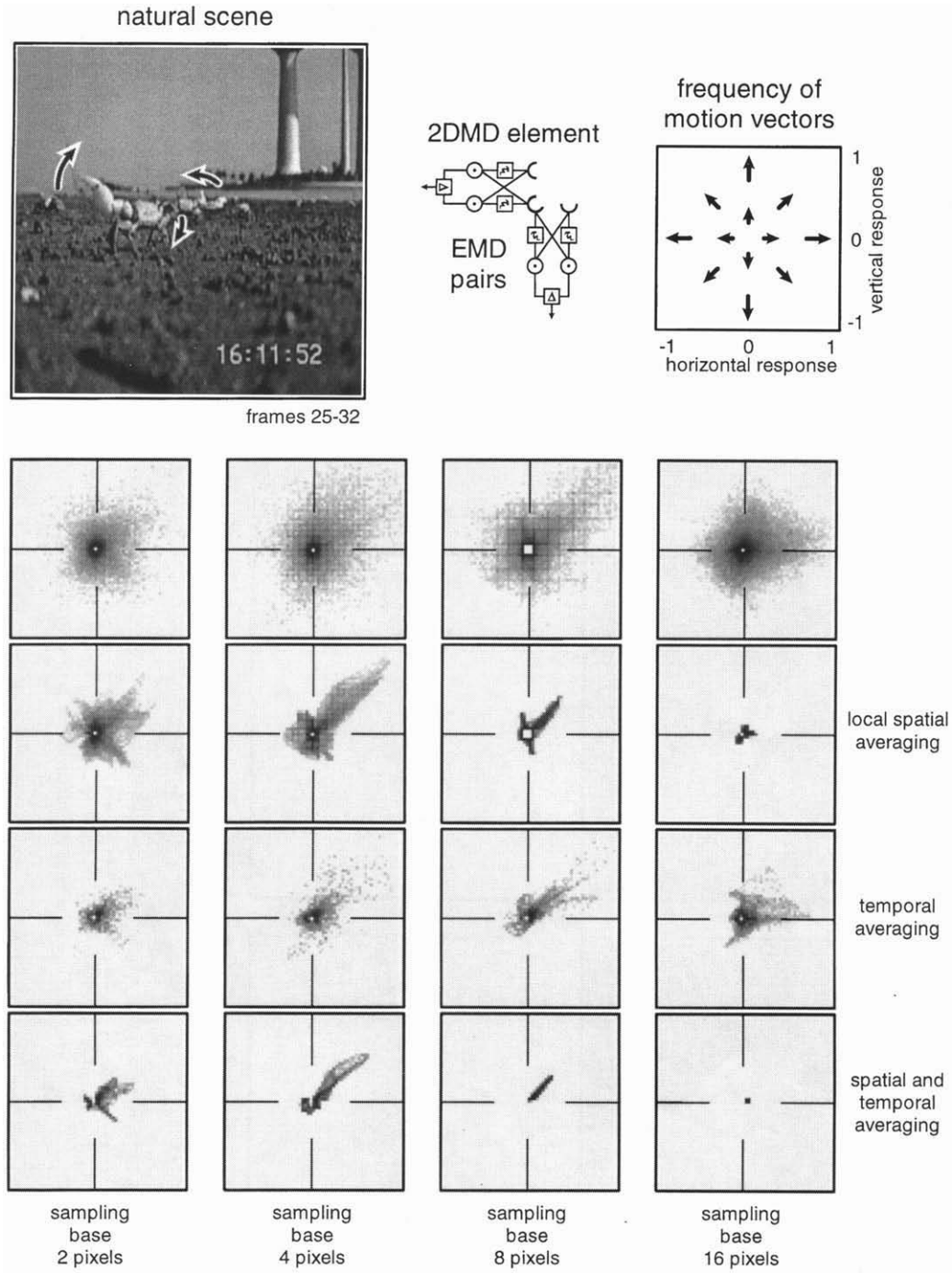

FIGURE 2. 2D-histograms of motion signals from a motion detector network (2DMD) consisting of orthogonal EMD pairs; each EMD combines the direct and the lowpass-filtered inputs (box with time-constant τ_L) from two neighbouring points in a multiplication (circle labelled ".") and subtracts two antisymmetric subunits (box "△"). An eight-frame sequence was used as input field (frame 4 is shown at top, arrows indicate the movements of crab limbs). Each panel shows in greylevel code, the number of responses within a given magnitude range for the various combinations of horizontal (abscissa) and vertical motion components (ordinate). Lines indicate respective zero responses (cf. schematic motion vectors in top right inset). The histograms thus represent directly the frequency of motion signals as a function of their magnitude and direction. Histograms are shown at four spatial scales along rows and along columns for the raw data, after local spatial averaging, after temporal averaging across all frames, and after the combination of both. Frequencies are plotted on a greylevel scale (with black indicating the highest number of occurrences, and light grey indicating the absence of a signal of a given direction and magnitude) as a function of these orthogonal components on the abscissa and ordinate, respectively (cf. arrows' length and direction in inset).

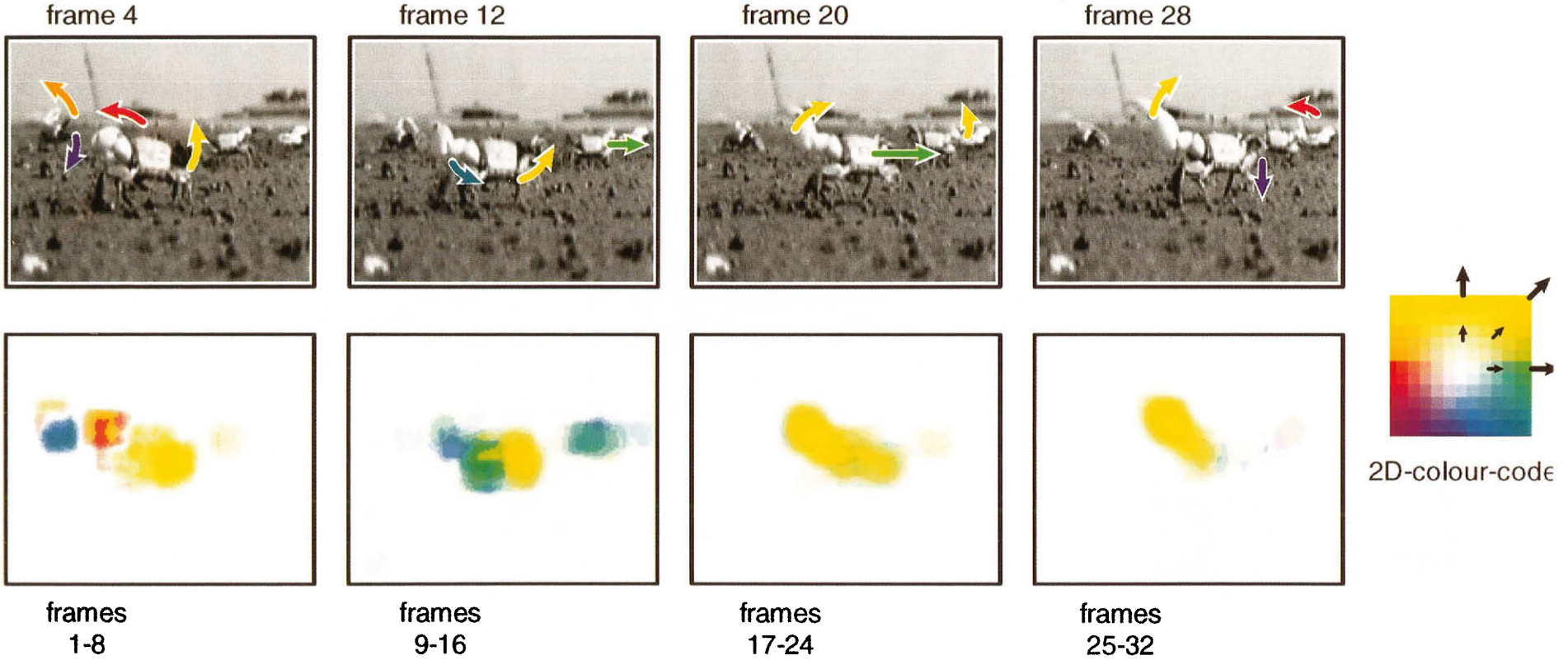

FIGURE 3. The spatial distribution of motion detector responses (lower row) in a 26 deg × 13 deg subregion of the original movie sequence (top row). Arrows in the still images indicate crab limb movements. Direction and strength of 2DMD output are represented in a 2D-pseudo-colour code with colour saturation indicating strength (white: no response) and hue indicating direction, as shown in the inset on the right (green: right, red: left, yellow: up, blue: down). The average over eight successive frames is shown for the spatially local average response of a 2DMD network with a sampling distance of 4 pixels.

respect, at least for the sequence presented here. Finally, the clearest image emerges when spatial and temporal averaging are combined (row 4 in Fig. 3), with the histogram for 4 pixels sampling distance showing a loop which possibly corresponds to the trajectory of the crab's claw. At the highest spatial resolution motion components in the lower right quadrant of the histogram become apparent which are caused by the crab lowering its walking legs. At the lowest spatial resolution the complete motion signal melts into one small dominant component corresponding to rightward motion of the whole crab, and all other details in the motion distribution are lost. On the other hand, at the highest spatial resolution, discriminating the various signal components from the overall noise is a demanding task. Comparing the different panels one gets the impression that a fairly good representation of the events in the visual scene is achieved with a resolution of about 4 pixels, corresponding to about 0.45 deg in vertical direction. This compares well to the optimum interommatidial angle of about 0.3 deg in this direction in the equatorial visual field of the crab. Looking at the overall motion distributions makes it clear that reasonable discrimination mechanisms require some spatial or temporal averaging, naturally at the price of losing spatial or temporal resolution.

So far, we have analysed the complete image without consideration of the spatial distribution of the motion signals. However, it is obvious in our example sequence that the relevant motion information stems from the left middle region of the images in which the crabs are moving, whereas motion signals from other parts of the image are distortions arising from instabilities. Indeed, the comparison of these two parts of the images leads to a better understanding of the events in the movie sequence (data not shown). The regional motion signal variations are best represented in the two-dimensional map of the 2DMD output. This is shown in Fig. 3 for the complete motion sequence featuring a series of events (indicated in the still images of the top row by arrows) which are clearly reflected by regions of corresponding motion signals (lower row, shown in 2D-colour code representing direction and strength by colour and saturation). For this figure, the motion signal is derived from a network with a sampling base of 4 pixels, which again gives a fairly accurate picture of the events in the movie sequence. For reasons of clarity the 2DMD output signals shown in Fig. 3 are averaged locally and temporally across the eight consecutive frames of the sequence. At other spatial resolutions similar patterns of motion responses are derived from the simulations (data not shown), with the expected gain and loss of spatial detail. Again, it is obvious that the visual system has to balance the need for clear and strong signals with the need for sufficient resolution of spatial relationships. As can be seen from the fair correspondence between the crab's actions and the 2DMD signals, this may possibly be well achieved at the highest spatial resolution available to the crab.

Figure 3 demonstrates that the relevant motion signals tend to originate from the regions close to the horizon. This specific spatial distribution of motion signals could be exploited systematically by neuronal mechanisms responsible for the detection of waving conspecifics. A strip of EMDs just covering the region above the horizon, and tuned to diagonal-to-horizontal swings of elongated objects, for instance, would be a simple device to detect the waving claws of signalling crabs of its own or other species. It is in the same part of the visual field, however, where predators need to be detected (Layne *et al.*, 1996). Following the idea of regional specialisations, it has to be considered how filters tuned to specific motions or motion patterns (across space and time) can help to extract clearly defined, behaviourally relevant events in a complex world of non-rigidly moving objects. A possibility is that detection and discrimination in crabworld scenes could be achieved with the kind of serially operating motion detectors proposed for the detection of higher-order motion stimuli (Cavanagh & Mather, 1989; Sperling, 1989; Zanker, 1995).

Are there specific strategies by which motion patterns could be labelled in the crab's visual system? There is some indication that fiddler crabs possess colour vision (Hyatt, 1975) and we know that they are most certainly polarisation-sensitive, at least in the dorsal visual field (Altevogt & von Hagen, 1964). Judging from what is known about the photoreceptors of other crustaceans (Shaw & Stowe, 1982; Cronin & Forward, 1988), it seems fair to assume that the spectral composition and the distribution of polarised light will be captured by the fiddler crab's eye in some detail. In addition to topographic and spatial cues, spectral and polarisation information may help crabs to segment motion patterns into contributions which are produced by predators, by conspecific males or by females.

Crabs with polarisers

Scenes in crabworld were recorded through a series of colour filters and through a rotating polariser. Not surprisingly, the saliency of relevant features varies in different parts of the spectrum. Substrate–sky contrast, for instance, is higher at short wavelengths compared with the red end of the spectrum (c.f. Wilson, 1978). Equally, the reflectance from the coloured parts of the crab's cuticle does differ when viewed through coloured filters. In the polarisation domain, however, there are surprises: Fig. 4 shows a large *Uca vomeris* male seen from the perspective of a juvenile crab through a horizontal (top) and a vertical polarising filter (bottom). The differences between the two images suggest that the distribution of direct and reflected polarised light can provide cues relevant to the detection and discrimination tasks we listed earlier. Light reflected from the substrate, for instance, is vertically polarised and reduces the contrast between the sky and the ground [compare Fig. 4(a) and Fig. 4(d)]. The system that detects the horizon line and keeps it aligned with the equatorial acute zone of the eye would at least under certain conditions have a much crisper signal to work with if it received light

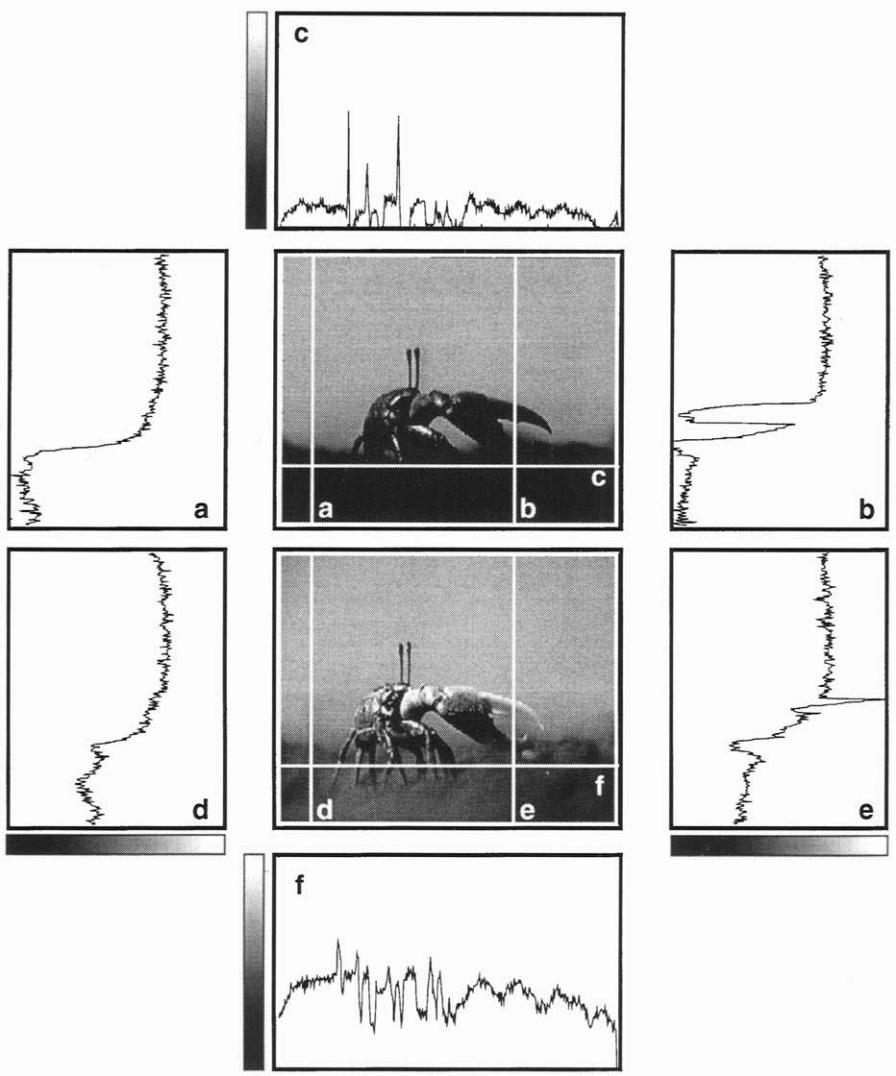

FIGURE 4. Two images of a fiddler crab through a horizontal (top) and a vertical (bottom) polarising filter. Transects (a)–(f) show the intensity values digitised with 8 bit resolution between 0 (black) and 255 (white) at different locations in the images.

through a horizontal polariser only. Object–sky and object–substrate contrast also differ in the two scenes. Except for the specular reflections, the cuticle of the crab returns more vertically than horizontally polarised light and the crab–sky contrast is consequently higher when the scene is viewed through a horizontal polariser [compare Fig. 4(b) and Fig. 4(e)]. The reverse is true for the crab–substrate contrast. Since neither substrate nor cuticle reflects horizontally polarised light, the legs or the carapace of the crab are barely distinguishable from the background. The large signals in the transect of Fig. 4(c) are caused by specular reflections from the cuticle of some of the legs. In the scene through the vertical polariser, however, legs clearly contrast against the lighter background [Fig. 4(f)].

This preliminary survey suggests that the analysis of polarised light in natural scenes may well be worth extending. There is a strong possibility that polarised light may play a role in communication and species recognition in fiddler crabs, as it does in cuttle fish (Shashar *et al.*, 1995) and possibly also in octopus (Shashar & Cronin, 1996). Polarisation effects are likely to depend on a number of factors like the wavelength of light, the time of day, the tidal cycle, the viewing direction and the surface moisture of crab cuticle. It will be interesting to see whether and how polarisation sensitivity can help crabs solve their diverse visual tasks.

CONCLUSIONS AND OUTLOOK

We have shown a few as yet rather qualitative views from the visual world of a particular animal to make the more general point that an ethological approach to scene analysis is needed and has become possible, given the right choice of animals and ecological setting. Our aim is to reconstruct the visual world of a crab. To this end we would need to reconstruct the available signals, their transformation by the sensory system and the visual tasks a crab has to perform. Our examples from crabworld are meant to argue that scenes are truly *natural* only from the animal-specific viewpoint and that their *statistics* are only meaningful when the ecological and the ethological

context are taken into account (cf. Passaglia *et al.*, 1995; Sedgwick, 1983). Both make the statistics of natural scenes non-stationary, meaning that the distribution of spatial frequencies, of wavelengths or of the direction and degree of polarisation cannot be assumed to be the same in different parts of the visual field (e.g. Field, 1994). The extent to which natural scenes contain local structure or have non-stationary statistics will furthermore be different in different animal species. By taking the ethological context into account we are also forced to define the *biologically relevant information content* of natural scenes which would seem to be the driving force behind the evolution of sensory filters and neural processing strategies (cf. Salmon & Hyatt, 1983).

Natural scene analysis has so far been rather general, by dealing with sets of images taken from a human observer's perspective to describe their statistics or to investigate optimal coding schemes (e.g. Field, 1994; van Hateren, 1992; Olshausen & Field, 1996). There is possibly a level of visual processing where correlating neuron properties to natural scene statistics can be done without having to consider the specific visual environments of animals (e.g. Srinivasan *et al.*, 1982; Laughlin, 1983; Field, 1994; van Hateren, 1992). However, recent comparative work has also reminded us of the essential point already made in pioneering studies (Lettvin *et al.*, 1959) that ecology and lifestyle do shape visual neurones' properties, from the level of photoreceptors (see, for instance Laughlin & Weckström, 1993; Osorio & Vorobyev, 1996) to higher levels of visual processing (O'Carroll *et al.*, 1996). What seems to be lacking at the moment—and what we would like to bring to the field of natural scene analysis—is quantitative access to the possibly crucial visual ecology of specific animals. It would be very interesting, for instance, to combine our ethological bottom-up approach with Olshausen & Field's (1996) technique to train networks for sparse coding that preserves the information inherent in animal-specific scenes. Such a combined strategy may eventually allow us to identify the subtle selective pressures that have driven the evolution of specifically tailored visual systems. As the first step in this direction, we presented here some aspects of how luminance profiles and motion content may be extracted from a dynamic natural scene, by using biologically plausible filter operations. The intrinsic limitations of neural filters, like those of correlation-type motion detectors, can help us to specify the actual detection and discrimination tasks of a visual system under natural conditions by analysing both their limits and possible processing stages that recover relevant information. The ethological approach to natural scene analysis will also provide material for putting theories of optimal coding to more stringent tests. If, for instance, it can be shown that the spatial frequency composition or the distribution of image velocities varies across the visual field of an animal, one could test whether the sensory and neural processing strategies in the *same* animal reflect this non-uniform stimulus situation (cf. Laughlin & Weckström, 1993; Jordan & Vogt, 1995).

In summary, we suggest that reconstructing an animal's visual world will contribute significantly to visual ecology. It forces us to consider environmental topography, the behaviour and biological context of animals and to develop means for defining the biological information content of natural scenes.

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Acknowledgements—We thank Colin Clifford, Martin Nagle and Mandyam Srinivasan for their critical comments on the manuscript. We are grateful to the Centre for Visual Sciences at the Australian National University for giving us the chance to work together and for providing the funds and the environment that make this collaboration possible.